1984 ~ (231)

Contributions of the Right Cerebral Hemisphere in Perceiving Paralinguistic Cues of Emotion[a]

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Abstract

Communication between human beings is mediated not only through verbal language: facial expressions, body gestures and intonational qualities of the voice all contribute to transmitting social cues, emphasizing or clarifying the verbal message, and communicating one's emotional state. To determine which brain structures might be critical for processing such information, subjects having either unilateral lesions or commissurotomy were given the PONS test, a standardized scale which assesses competence in decoding paralinguistic cues. Our results indicate that overall sensitivity to nonverbal communication is more reliant upon structures the right cerebral hemisphere than the left, and is thus processed on the opposite side of the brain from verbal language. The right hemisphere appears to be particularly critical for evaluating facial expressions, the most salient channel of emotional communication.

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[a]Adapted from an article written for the McLean Hospital Journal, 3/4:146-167, 1980

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I also wish to thank Dr. S. Weintraub and Ms. Robin Baratz (Behavioral Neurology Unit, Beth Israel Hospital) and Dr. Edith Kaplan (Boston Veterans' Administration Hospital) for kindly providing us with subjects and with neuropsychological assessments. The research was supported by a Sloan Foundation Fellowship to the first author.

Discoveries in neurology and linguistics indicate that many aspects of human language are determined by specific structural features of the brain, a notion which differs radically from the more prevalent idea of language being an arbitrary, culturally evolved set of symbols and combinatorial rules which during development somehow become represented upon an infinitely malleable nervous system. The present study has attempted to examine whether such neurological specification might extend to other aspects of our social interactions as well, particularly the communication of affect through paralinguistic cues. But before describing the rationale for our own studies, it might be best to mention a little more about spoken language.

Through postmortem studies of people who, during their lives had lost linguistic fluency after stroke, the French neurologist Paul Broca discovered that it was the left inferior precentral cortex whose destruction caused speech production to be very labored, with most grammatical elements omitted. In this disorder, now commonly known as Broca's aphasia, the principal content words remain appropriate but are produced with difficulty. Full sentences are seldom used, and surprisingly, reading or repetition of text material follows the same pattern. Singing remains intact, however, showing that the dysfunction is not general to all vocal control. Rather, it has been postulated that Broca's area is involved in transforming intentions or ideas into spoken utterances according to the appropriate grammatical rules.[1] A few years after Broca's discovery, the German neurologist Carl Wernicke found that damage to another portion of the left hemisphere, adjacent to the primary auditory area in the temporal lobe, is associated with a disorder in which speech production is fluent but often makes little sense. Nonsensical words are included, incorrect syllables are substituted in otherwise correct words, and ideation is sometimes aberrant. Grammatical form is intact, however, and even the inappropriate words take on a syntactic form suitable to their place in the sentence. Phrase length and melody of speech are preserved, so that someone not familiar with the language being spoken would have the impression that all is normal. Comprehension of spoken or written language is likewise impaired, and it is believed that Wernicke's area may play a role in processing semantic and ideational aspects of language. Other types of language disorders, including selective losses in reading, repetition, and naming, have likewise been associated with the loss of particular left brain regions, supporting the idea that human language is inexorably related to specific anatomical features of the brain. Moreover, recent studies now indicate that portions of the posterior temporal cortex, which includes the Wernicke's

area, are asymmetric between the two sides of the brain at birth.[2] Thus, it may be the case that the neurology may even prefigure where and how language becomes represented in the brain, or, in other words, our linguistic abilities may actually be the product of highly specialized, predetermined circuits in the brain. A similar conclusion has been reached by linguists impressed with the many stereotyped features of language development in the child and with the universality of formal aspects of syntax.[3,4] Language develops without the child needing any explicit instruction as to rules of phenome production or syntax, a phenomenon which Chomsky[3] has argued can only come about by linguistic competence being predetermined by the neurology of the human brain. Chomsky has also argued that other domains of human cognition which are similarly acquired spontaneously in childhood and which are universal in their manifestation must likewise reflect well-defined neural determinants. One faculty which may be of this nature would be the ability to evaluate the significance of paralinguistic cues in communication.

As demonstrated in numerous studies, a great deal of the information which is exchanged in human interactions is not contained in the words alone as they would appear in a written text: facial expressions, body movements and intonational qualities of the voice all serve to structure and qualify the verbal message, influence the social relationship between speaker and listener, and convey information about one's emotional state.[5-10] The thesis that competence in evaluating these cues may be specified by our biological inheritance was first put forth in 1872 by Charles Darwin. "The Expression of the Emotions in Man and Animals," presents a series of observations, arguments, and proposals for further research which stand today as the most thorough analysis of the biology of affective communication. Darwin was particularly impressed with the observation that the facial expressions that appear during such states as anger, disgust, and pleasure appear in infancy and are universal to all cultures. He carefully analyzed the groups of facial muscles involved in the formation of these expressions, then reasoned how such activational patterns might have selectively come to be "hard-wired" because of their functional advantages in our evolutionary past. And while their actual utility would have long since disappeared, the patterns of expression may have been retained for their communicative value. However, for this to be of any significance, not only the expressive capacity, but also the ability to perceive the significance of these signals would need to be specified biologically. By analogy with spoken language, where some 2000 distinct tongues exist and where almost no words are

universal, the issue is not whether the particular signals used are common, but whether formal features of the communicative system are. Yet unlike spoken language, many facial expressions, body movements, and vocal intonations used to express particular emotions are indeed identical between cultures that have been separated from one another for thousands of years, presumably because the fixed neuromuscular patterns that are involved. But aside from these instances of emotional expression, much of nonverbal communication is quite culture-specific, composed, according to Birdwhistell,[9] of a hierarchy of elements which can be compared to phonemes, words and sentences.

In the present study we examined whether the ability to evaluate the emotional significance of paralinguistic cues might be associated with specific cortical regions. Subjects having well-defined patterns of brain damage, including either lateralized lesions or surgical commissurotomy, were given a standardized test in identifying facial expressions, body movements and intonational qualities of the voice. The principal question was whether these abilities are well localized, as is the case for spoken language, or whether instead they are more diffusely represented in the brain. A priori, one might imagine that nonverbal communication could be closely allied in the brain to language, since paralinguistic cues accompany the verbal message and, like it, require the interpretation of discrete symbols. Alternatively, it might be anticipated that nonverbal communication might be more a function of the right cerebral hemisphere, since it is that side of the brain which is dominant for such functions as distinguishing faces, apprehending spatial relations, processing certain features of music, and perhaps even responding appropriately to emotional situations.[12] Another question was whether the various aspects of nonverbal sensitivity were dissociable from one another, i.e., whether each represents a discrete function unto itself, and further what other cognitive faculties these abilities might be related to.

Subjects

The 11 subjects used in the first set of studies had predominantly unilateral brain lesions which had been verified radiographically (10 by CT scan and one by angiography): EEG data were also available in several cases. Table 1 summarizes the neurological and behavioral data on these subjects, obtained by staff members of the Beth Israel and Boston Veterans' Administration Hospitals.

The PONS Test

The test used for these studies, the Profile of Nonverbal Sensitivity (PONS), was developed by Professor Robert Rosenthal and his colleagues in the Department of Psychology, Harvard University.[13] The PONS is a standardized scale designed to assess competence in interpreting various types of emotional scenes presented through facial expressions, body movements and intonational qualities of the voice. The test has been administered to several thousand people in this country and elsewhere, providing extensive normative data against which the performance of our neurological subjects could be compared.

The PONS consists of a 16 mm black-and-white film containing 220 items to be discriminated. Each item runs for two seconds and portrays one of 20 different scenes presented through one or more channels of nonverbal communication. The 20 scenes used in the PONS test were portrayed by a young woman and vary in emotional tone along two dimensions, positive-negative and dominant-submissive.

Each of the scenes is presented in 11 different ways, varying according to the channels of information available. Five of these contain only "pure" visual or "pure" audio information: (1) face alone, no voice; (2) body from neck to knees, no voice; (3) face plus body, no voice; (4) random-spliced (RS) speech, no picture; (5) electronically filtered speech (called CF, or content filtered). The remaining six modes represent combinations of these: (6) face plus random-spliced speech; (7) face plus content-filtered speech; (8) body + RS; (9) body + CF; (10) full figure + RS; and (11) full figure + CF. Items depicting various emotional scenes through different channels appear in random sequence on the test.

To prepare the random-spliced speech, the two-second audio tape was cut into small segments and randomly reassembled. When played back, tonal qualities of the voice are retained but the sequence of individual sounds is disrupted. In content-filtered speech, selected bands of frequencies are removed and the audio signal is clipped. Although the voice sounds muffled and unintelligible, the intonation, rhythm, tempo and loudness of speech are preserved. In a sense, the random-spliced speech and the content-filtered speech can be viewed as being somewhat complementary. The random-spliced speech retains tone and timbre but degrades the rhythm, while the content-filtered speech loses the tonal qualities of the voice but retains the rhythm or sequence.

After ascertaining that the oral instructions for the test were understood, visual functioning was demonstrated by having subjects read the film credits on the screen and, intermittently during the test, asking them to describe the actress's poses. For the test items, the viewer selects one of two alternative choices which best describes the scene presented. These two choices — the correct one and a randomly selected incorrect one — normally appear on an answer sheet. However, since many of the neurological subjects were either dyslexic, hemianopic, or suffered hemifield neglect, the choices were read aloud to them before the scenes appeared. When requested to do so by the subjects, the choices were again repeated after the scenes, though this was kept to a minimum to avoid possible cueing by the experimenter's voice intonation. General alertness and attention to the test were monitored throughout. The strongest assurance of adequate comprehension and response set, however, was the observation that each subject was able to obtain normal scores on one or more portions of the test.

Data

Test results are reported in terms of percentile rankings, obtained by comparing subjects' raw scores with the published normative data.[14] On the various channels of nonverbal communication, data are pooled together to increase the size of the item samples. Thus, for the first channel presented in Table 2, "Audio only," the score for the 20 items in which CF speech was presented without any visual information plus the score for the 20 items in which RS was presented without any visual informa-

tion are pooled together. Each of the next two columns, RS and CF, combines the score for the 20 items in which the audio channel was presented alone plus the 60 in which it was combined with either the face, body, or whole figure. On the visual items, "Face" includes the 20 items in which the face was shown alone plus the 40 items in which it appeared together with RS or CF speech. "Body" and "Figure" are similarly derived. "Video only" shows the score for the 60 items in which the face, body, and full figure were presented without any audio information. The right side of Table 2 presents subjects' performance analyzed by the type of scene: scores are based upon the 55 items for each emotional quadrant (ie, positive-submissive, positive-dominant, negative-submissive and negative-dominant).

Results

Several of the most interesting cases will first be presented individually; general comments about the overall performance of right- vs. left-brain-damaged subjects follow.

A. *Right-Brain-Damaged Subjects*

R1. This 56-year-old man suffered a stroke of the right middle cerebral artery six months prior to testing, which resulted in an infarct of the right temporal and inferior parietal areas. He had previously held a position of considerable responsibility in a large company, while also finding time to read several books a week. After the stroke, R1 was no longer able to get the gist of what he was reading, but described this simply as a "vision problem." Subsequent tests showed his acuity to be normal, although a left inferior quadrantanopia and some left visual field neglect were noted. Deficits were found in color-naming, judgment of distances, and object recognition. A striking personality change was also noted: his formerly reserved, gentlemanly demeanor disappeared and he became quarrelsome, joked continuously, often about sexual subjects, and was noted as acting inappropriately familiar with staff members. Language usage remained rich; his posttraumatic verbal IQ was 135, performance 102.

On the PONS test, R1's overall score fell three standard deviations below normal. Performance was particularly impaired on the items involving facial expressions, and when only

the face was shown he scored randomly. In striking contrast, he was normal on items requiring judgment of body gestures alone. An extraordinary feature of this man's performance was that, despite his inability to evaluate facial items, the face nevertheless appears to have remained magnetic to him and stood in the way of his making use of other cues whenever it was present. If we consider the test items in which the face was absent (ie, body alone, tone-only items, BO + CF speech, etc.), this subject actually scored fairly well, performing only 0.83 standard deviation below normal; however, when the face was added on to these channels his performance fell another two standard deviations.

On audio items, R1 was 3.2 standard deviations below normal on items containing random-spliced speech alone, but only 1.6 standard deviations below normal for content-filtered items. When his performance was analyzed across the different types of scene, a very skewed profile appeared: while he was only one standard deviation below average in recognizing dominant items, particularly negative-dominant ones (eg, expressing anger), he was practically incapable of properly identifying positive-submissive items (eg, asking forgiveness).

R5. This 59-year-old man suffered two strokes five and eight years ago: CT scans reveal focal atrophy in the right parietal area, along with some dilatation of the right lateral ventricle and temporal horn. Continuing seizure activity in the right hemisphere was revealed by an EEG. Formerly a factory owner and manager of two restaurants, R5 lost much of his drive after the two strokes. **However, he remains articulate and continues to speak three languages fluently. He is very sociable, humorous, and warm.**

Striking visuospatial deficits are apparent: though he can copy figures well, he has poor memory for designs and is highly disoriented spatially. He has little ability to remember faces; he reports having spoken to people for hours, then having no memory of them or of the conversation the next day. A left hemifield inattention was noted in the neurological exam.

On the PONS test, R5's overall performance was a little over one standard deviation below normal. **Unlike** R1, his ability to identify facial expressions was fully intact. He scored less well on items showing the body only, and was extremely poor in judging intonational qualities of the voice (on items **that included the**

voice only, he scored at a nearly chance level). Across the various types of emotional scenes, he showed a skewed performance profile reminiscent of R1's. R5 was adept in identifying negative-dominant items, but was poor in evaluating positive emotional scenes.

R6. Ten months previously, this 71-year-old man suffered two massive strokes in distribution of the right middle cerebral artery, resulting in a severe atrophy of the temporoparietal area. A dense left hemiplegia and hemaesthesia remain, as does a neglect of the left visual field. This eminent surgeon had been admitted to college in his youth on the basis of having one of the highest Stanford-Binet scores in the country. His WAIS verbal IQ remains 148 after the stroke, although his performance score is down to 89. Writing and reading remain intact, although inconsequential words in the left hemifield are occasionally omitted. Language usage, especially in describing remote events, is rich in detail and humor, though produced in a somewhat deadpan, monotonous manner. Digit span and simple arithmetic are normal. However, verbal abstraction is poor. Performance on block design, picture arrangement, object assembly and digit symbol tasks are all severely compromised, as are copying and drawing from memory. A left hemineglect is dramatic, although this is more marked for designs than for reading words. Recognition of famous faces is somewhat impaired, but faces on the ward are recognized. Facial mimicry is poor. Singing is monotonous with rhythm preserved. The subject has been incontinent and has occasionally been seen exposed on the ward. He is unaware of his visuospatial and other cognitive problems.

R7 was only able to complete half of the PONS test, and consequently the scores reported in Table 2 represent extrapolations which are somewhat less statistically reliable than for the other cases. Overall performance was 3.5 standard deviations below the norm (0.02° percentile), with the deficit being greater for video than for audio channels. Across the various types of scenes, identification of positive-dominant items was just outside the normal range; in contrast, negative-dominant items, normally the most salient on the test, were barely recognized at all.

B. *Subjects with Damage to the Left Hemisphere*

L1: This formerly right-handed, 27-year-old man suffered an

occlusion of the left carotid artery at the age of six which resulted in a dense right hemiplegia and a severe language deficit. The right side remains spastic and atrophic, and the subject now relies upon his left arm. However, no right hemianopia or loss of sensation are observed. The subject reads at a grade 4 level, writes at a primer level, misspells the simplest words and cannot do simple arithmetic operations. Vocabulary is at a grade 6 level. Grammar is somewhat restricted but correct. Some difficulty in word-finding and in pronunciation remain. Prosody is good. Moderate to severe deficits are seen on tests of motor organization and sequencing. Constructional ability and recall of complex figures are good. WAIS verbal IQ is 100, performance 103. Dilantin and pentobarbitol are taken to control seizures.

The subject's overall performance on the PONS test was slightly above average. Excellent scores were obtained on video items, particularly those involving the face. Performance for items with audio information only was considerably inferior, although all scores fell within one standard deviation of the mean. For the different types of scenes, the negative and submissive items were perceived exceptionally well, the others within the normal range.

L4, a 49-year-old right-handed man, suffered an aneurism of the left internal carotid with a cerebrovascular infarct in distribution of the left middle cerebral artery two years ago. Shortly after the stroke, speech was fluent but empty of content. The subject could follow orders but could not point to objects or repeat even single words or numbers. Comprehension has improved markedly, although a few words are still missed. Speech is halting, contains paraphasias of phonetically or semantically related words, along with circumlocutions, agrammatisms, and some neologisms. Intonation of speech is good. Visuospatial and constructional abilities are unimpaired. Performance IQ on the WAIS is 144, and even shortly after the stroke, the subject scored in the 95° percentile on the Raven's progressive matrices test.

Overall performance on the PONS test was just below average (38th percentile), and scores on all items fell within ± 1 standard deviation of the norm. Across the various types of scenes, scores range from the upper quartile for recognition of the negative-dominant scenes to the lower quartile for both positive-dominant and negative-submissive items.

C. *General Comparison of Right- and Left-Brain-Damaged Groups*

The left- and right-hemisphere groups both comprise heterogeneous populations, not only in terms of the subjects' age, sex, background, and native intelligence, but also in terms of the specific loci of damage within the hemisphere. Nevertheless, certain between-group differences stand out markedly. In overall scores, the subjects with right-sided damage averaged 1.86 ± 0.40 standard deviations below the mean, the subjects with left-sided damage 0.48 ± 0.33 standard deviation below; these differ at a level of $0.05 > p > 0.01$ (2-tailed). Comparing the two groups' performance on the various channels, the subjects with right-sided damage were significantly poorer in interpreting random-spliced speech ($p \sim .02$), and, most strikingly, facial expressions ($p \sim 0.01$). No reliable between-group differences were found for recognition of body expressions ($p \sim 0.15$), content-filtered speech ($p \sim 0.25$) or tone only.

Differences between the two groups were marginally significant for items involving the whole figure ($p \sim 0.08$) and video alone ($p \sim 0.07$), effects very likely attributable to the inclusion of facial expressions in both of these categories.

The scoring profiles of the two groups suggest a complementarity in their patterns of deficits. On visual items, subjects having right hemisphere damage did relatively better in discerning emotions from the body gestures than from the face; with audio input, they were relatively better with content-filtered than with random-spliced speech. The data from the left-hemisphere subjects suggest just the opposite pattern: better performance of items of facial expression than for body gestures, and higher scores for RS vs CF speech. In comparison with the subjects having left-sided damage, the right hemisphere group's relative impairment in discerning facial emotions more than body gestures is significant at a p value of 0.05 (2-tailed), and for audio information the relative impairment in interpreting random-spliced more than content-filtered speech is reliable at the $p = 0.07$ level (2-tailed).

While most individuals in both groups tended to show highly skewed profiles across the different types of emotional scenes, no overall between-group differences stood out when scores were pooled.

D. Studies in "Split-Brain" Subjects

Working in the laboratory of Dr. R.W. Sperry at Cal Tech, we administered the PONS test to several "split-brain" patients, people whose two cerebral hemispheres function in isolation from one another following surgical resection of the tencephalic commissures.[12] Studies in these subjects have of course already provided us with invaluable information about the contributions of the two hemispheres in many cognitive domains, and we felt that these people would allow us an extraordinary opportunity to further examine the cerebral lateralization of nonverbal communication.

In these subjects we used a shorter version of the PONS containing 80 items: a film showing the 20 "face only" items and the 20 with body alone; and an audio tape which presented the 20 RS and 20 CF speech items.

Very dramatic results were obtained from subject LB, a 24-year-old right-handed man who had been commissurotomized at the age of 13 for intractable epilepsy. His WAIS verbal IQ is 110, performance 100. On visual items of the PONS test, each hemisphere was tested separately using the newly developed "Z-lens."[16] This system is composed of a collimator attached to a contact lens. By covering one eye and occluding either the nasal or the temporal half of the collimator, complex visual stimuli can be presented over long periods of time to only one hemisphere, an advance which for the first time allows the limits of competence of each side of the brain to be studied in isolation. The right hemisphere was tested first so that any practice effects, though unanticipated, would be to the advantage of the left hemisphere. To obtain the response of the mute right hemisphere, the subject was asked to use left hand signals to indicate which of the two choices read to him he preferred. On video portions of the PONS test, LB's right hemisphere scored perfectly normally on the items showing facial expressions (ie, in the 50th percentile), but only at the 5th percentile level for body movements. The isolated left hemisphere showed just the reverse pattern: using verbal responses to indicate his choices, LB now scored in the 26th percentile for body movements but only at the 4 percentile level on facial expressions.

Since audio information presented to either ear gets projected to both cerebral hemispheres, it was not possible to lateralize the vocal items of the PONS test. We nevertheless attempted to assess each hemisphere's performance, either by having the contralateral hand use finger signals to indicate which choice was preferred, or in some cases, by allowing the hand to select by touch a plastic number 1 or 2 from an array of six plastic numbers. With this method, subject LB scored very well on both RS and CF items using either his left hand or a verbal response to indicate his choice.

In three other split-brain subjects who were studied, it was not possible to lateralize the video portion of the test (contact lenses have not been made to fit two of these subjects, and a third who does have a lens was completely inattentive when the right hemisphere was tested). Viewing the test in free vision and making verbal responses which presumably reflect the choices of the left hemisphere, two of the three scored equally poorly on both face and body; the third subject scored normally on body movement items but in the bottom percentile on facial expressions. On audio items, one subject showed a striking superiority for CF speech over RS, while the other two did not show much of a difference between RS and CF when giving verbal answers.

Another remarkable subject tested at Cal Tech was DW, a 20-year-old man who underwent a right hemispherectomy at the age of eight. His WISC verbal IQ has been measured as 80, performance 60. On the PONS test, he scored at a purely chance level on facial expressions, but in the 26° percentile on body movements. On audio portions of the test, DW scored in the 82° percentile on content-filtered speech items, but only in the 16° percentile for RS speech. Since this subject only possesses a left hemisphere, these results are quite unambiguous with respect to which side is controlling the response.

Discussion

The first conclusion to be drawn from these results is that sensitivity to nonverbal communication is largely dissociated in the brain from verbal abilities, the two domains [illegible] requiring opposite hemispheres. This dissociation is particularly evident in right-brain-damaged subjects R1 and R7. Both of these

men scored nearly three standard deviations below normal on the PONS test, but retained posttraumtic verbal IQ's more than two standard deviations above normal. In contrast, subject L1, whose extensive left hemisphere damage early in life left him with a number of severe language-related problems, scored above average on the test. It might be noted that despite the relatively small population tested here and the variability among the sites of damage, the performance difference between the right and left hemisphere groups nevertheless achieved statistical significance, a testimony to just how clear a right hemisphere function overall sensitivity to nonverbal communication is.

Facial expressions normally convey the greatest amount of information in nonverbal communication[10,17,18] and it is their inability to evaluate these signals which presents the greatest problem for most of the right-brain-damaged subjects. Five our of seven patients in this group scored in the 4° percentile or below on items showing facial expressions alone.

The right hemispherectomy patient also scored at a chance level on these items, while the split-brain subjects tested with their left hemisphere did only slightly better. Conversely, the one split-brain subject who was tested with his right hemisphere alone performed quite well on facial expressions, as did all of the neurological subjects having left-sided lesions but an intact right hemisphere. Thus, all of the data indicate that it is the perception of facial expressions which is particularly lateralized to the right hemisphere. In the right hemispherectomy patient, the persistent inability to evaluate facial emotions despite the passage of 12 years since surgery would further suggest that the left hemisphere may possess little potential to acquire facial emotional recognition. Further support for this thesis would require studies in cases where right hemispherectomy had been done even earlier than age eight.

A superiority of the right hemisphere in the recognition of different faces is well established[19,20] involving in particular the right occipitotemporal region,[21,22] and for learning new faces, the hippocampal and parietal areas as well.[23,24,25] Prosopagnosia, a relatively pure inability to recognize faces but not other familiar visual objects, has been associated with lesions of the right occip-

itotemporal area (lingual and/or fusiform gyri), combined with damage to related (usually homologous) structures on the left side of the brain.[26]

In the present group of subjects, the region that appeared to be the most critical for identifying facial emotions may be somewhat coextensive with that involved in facial recognition: a comparison of the lesion sites for subjects who did relatively well or poorly in judging facial expressions would suggest that it may be the right temporal area that is particularly important for "reading the face." This raises the question of whether the deficit reported here may not be part of a general prosopagnosia. However, among the subjects who scored poorly in evaluating facial emotions, all but one were clinically unimpaired in distinguishing faces; conversely, the one right-brain-damaged subject who did well in recognizing facial expressions (R5) reported great difficulties in remembering new faces. Differential impairments in physiognomic vs emotional recognition of faces have also recently been reported in another study of right-brain-damaged subjects.[27]

And in normal subjects, studies using tachistoscopically presented faces suggest that the perception of facial emotions is more strongly lateralized as a right hemispheric function than is the ability to identify individual faces. Several earlier studies had shown that faces presented tachistoscopically to the left visual field (i.e., directly to the right hemisphere) are recognized somewhat faster than when presented to the right visual field, although this difference is minimal for familiar faces.[28,29,30] When the task is to recognize *emotions* in the face, however, the superiority of the right hemisphere becomes considerably more pronounced. For facial emotions, the reaction time difference for the right vs the left hemisphere is twice that obtained when the faces are nonemotional,[31] and another study reported that the right hemisphere's **superiority over the left increases systematically with the intensity** of the emotions depicted.[32] Also, in split-brain subjects, Levy et al[20] have shown that while the right hemisphere is superior to the left in distinguishing different faces, the left side is quite competent as well, particularly when readily nameable features are available (eg, glasses or a moustache). In contrast, the present studies, some of which were done in the same split-brain subjects, indicate practically no left hemispheric ability at all for recognizing facial emotions.

In contrast to facial expressions, the evaluation of body movements does not appear to be lateralized as a right hemispheric function. Four of the right-brain-damaged subjects scored at least 1.5 standard deviations higher in judging body movements than facial expressions, and in the split-brain and hemispherectomy subjects, the left hemisphere showed a far greater ability in judging body movements than facial emotions. Conversely, in the one instance where the right hemisphere was tested alone, it did much poorer with the body than with the face. At this point, the basis for a differential lateralization in judging facial expressions and body movements can only be a matter of speculation. Perhaps it is because the body movements are more conventionalized sequences of specific symbols in time, and thus more the métier of the left hemisphere. Other studies have shown that losses of gestural and pantomimic abilities are associated more with left than with right hemisphere damage,[33] as are deficits in interpreting gestures.[34] The perception of emotion-specific body movements seems not to have been explored as thoroughly, although it might be noted that losses in overt emotional expression have been linked with right parietal damage.[35]

On the audio items of the PONS test, the patterns of impairments shown by our subjects suggest the possibility that two distinctive qualities in the voice may be processed differentially in the two hemispheres. That is, the right hemisphere may be relatively more concerned with processing timbre and tonal contrasts of the voice (which are retained in RS speech), whereas timing or rhythmic qualities (which are preserved in CF items) may depend more upon the left side of the brain. Such a dichotomy would be consistent with the observation that in music, discrimination of tone and timbre are more sensitive to right than to left temporal lobectomy,[36] while rhythm appears to be better represented on the left side of the brain.[37] It should be emphasized, however, that counterexamples to this dichotomy can be found among the present group of subjects: eg, several right-brain-damaged subjects scored as poorly on CF items as on RS, while one subject with a right temporal AVM scored very well on both RS and CF speech. Thus, any conclusions reached about the

Considering the importance of nonverbal communication for such things as mother-infant interactions, establishment of social hierarchies, minimization of physical conflict, and group coherence, it does not seem unreasonable to imagine that specific neural determinants have evolved to specify competence in this domain. In certain neurological patients, particularly those suffering lesions of the right hemisphere, damage to these centers could lead to major perceptual and behavioral limitations and may be related to the crippling interpersonal and emotional changes which have often been described after such brain damage.[50] It would seem that the routine inclusion of tests for nonverbal sensitivity in the neurological examination might help bring to light important dysfunctions, while also contributing to our general understanding of brain-behavior relations.

Note: This work was done in collaboration with David Bear, M.D. (Department of Psychiatry, Harvard Medical School and Behavioral Neurology Unit, Beth Israel Hospital); Marsel-M. Mesulam, M.D. (Department of Neurology, Harvard Medical School and Beth Israel Hospital); Robert Rosenthal, Ph.D. (Department of Psychology, Harvard University); Eran Zaidel, Ph.D. (Department of Biology, California Institute of Technology); and Roger W. Sperry, Ph.D. (California Institute of Technology). The research was supported by a Sloan Foundation Fellowship to the author.

I also wish to thank Dr. S. Weintraub and Ms. Robin Baratz (Behavioral Neurology Unit, Beth Israel Hospital) and Dr. Edith Kaplan (Boston Veterans' Administration Hospital) for kindly providing us with subjects and with neuropsychological assessments.

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roles of the two hemispheres in processing various qualities of the voice must be considered very tentative. Previous studies in this area have generally not separated the contributions of tone vs timing, but have instead presented emotionally intonated neutral or foreign material, either to neurological subjects or to normals using dichotic listening. While most of these studies have suggested an overall right hemispheric superiority in judging emotion in the voice,[38-42] others suggest an equal involvement of the left hemisphere.[43,44]

The inability of right-brain-damaged subjects to assess the emotional significance of items on the PONS test is consistent with many earlier observations. Denial and unconcern about their illness, indifference to previously significant details or people, inappropriate reactions to abstract, emotional or humorous stories, continuous joking, and inappropriate social behavior have all been described in association with right-brain damage.[12,45-49] As noted in the descriptions of the individual cases here (Table 1), all but one of the right-brain-damaged subjects tested showed some of these characteristics. However, somewhat surprisingly on the PONS test most of our subjects appeared to have idiosyncratic patterns of emotional apperception selective to certain types of scenes. R4, for example, who was strikingly insensitive to his family's anger towards him, scored in the lowest 1% in evaluating negative-dominant items but was in the top quartile in evaluating positive-dominant scenes. R5, in contrast, scored in the 69° percentile for judging negative emotions but did poorly for all positive items. In all, five out of seven right-brain-damaged subjects had scores which spanned more than two standard deviations across the different emotional quadrants. And while subjects with left hemisphere damage generally scored higher overall on the PONS test, they too showed great variability in their perceptions of different emotions. At this point we are unable to determine whether these results reflect exaggerated aspects of subjects' premorbid personalities, interpretive problems resulting from each subject's particular pattern of perceptual changes, or differential alterations of neural substrates underlying various emotional associations.

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